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Evaluation of moth-trap data from Alice Holt Forest, Hampshire, 1966–2001: possible effects of changing climate on Macrolepidoptera

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Introduction

As well as changes to the current distribution of trees and the composition and the character of woodlands (Berry *et al.*, 2002), climate change is expected to affect forests indirectly by modifying the distribution and abundance of insect herbivore species (Evans, Straw & Watt, 2002). Native and non-native trees in the U.K. are defoliated by several species of Macrolepidoptera, for example *Operophtera brumata* (Linnaeus), *Erannis defoliaria* (Clerck), *Agriopis aurantiaria* (Hübner) and *Alsophila aescularia* ([Denis & Schiffermüller]), and it is expected that climate change will alter the timing of life-cycle events and the frequency, intensity and duration of outbreaks (Department of the Environment, 1996; Cannon, 1998). Past outbreaks have caused localised and sometimes severe and prolonged defoliation (Anonymous, 1979; Packham *et al.*, 1992; Harding, 2002).

Several authorities, e.g. Kuchlein & Ellis (1997), Woiwod (1997), Virtanen & Neuvonen (1999) and Evans, Straw & Watt (2002), have suggested that climate change is likely to favour the survival and spread of Lepidoptera in the U.K. and alter their pest and conservation status. In contrast, Conrad, Woiwod & Perry (2001) showed in a study of *Arctia caja* (Linnaeus) that warmer and wetter winters and springs attributable to global warming might be directly related to the decline of this species in the U.K. This may be part of a more general decline in moth numbers across the U.K. (Woiwod, 2003) and elsewhere in Europe (Szentkirályi, Kazinczy & Leskó, 2001).

It is difficult to reconcile decline with the general consensus that future climatic conditions are expected to facilitate increases in species diversity and abundance, and therefore potential pest risk. For Lepidoptera, predictions about range expansions and migrant invasions are generally based on knowledge of the relationship between their biology and climatic variables, particularly temperature and precipitation (Warren, Pollard & Bibby, 1986; Turner, Gatehouse & Corey, 1987; Pollard, 1988). However, phenological asynchrony between host and herbivore (Dewar & Watt, 1992; Cannon, 1998; Visser & Holleman, 2001; Ivashov, Noyko & Simchuk, 2002), and changes in the palatability of vegetation resulting from the increased uptake of carbon dioxide by trees from an atmosphere enriched with greenhouse gases (Buse *et al.*, 1998) may compromise the ability of herbivores to capitalise upon a favourable climate.

Changing agricultural practices, habitat management and loss of habitat have also been implicated as factors in the decline of Lepidoptera in the U.K. (Asher *et al.*, 2001). Twenty years of recording Lepidoptera in the New Forest has shown a dramatic decline that may be attributable to increasingly high levels of grazing and browsing (Green, 2001). Such factors may act together to counter and therefore obscure possible favourable effects of climate change on Lepidoptera populations.

Robust predictions about changes to Lepidoptera populations under future climate scenarios are therefore important to assess and manage the long-term health and productivity of woodlands and forests. Tracking trends in local species demography provides an opportunity to relate community-wide changes to changes in environmental conditions, and to test hypotheses about the relative impact of habitat disturbance and climate change. In the present study, the records of Macrolepidoptera collected over 36 years at one site in the south of England have been summarised and used to examine trends in species abundance and numbers of species occurring in relation to local climatic data. Particular attention was given to those species that are known to favour broadleaved trees for food, in order to identify how the health and the productivity of these trees might be affected in the future.

Methods

Study site

The data were collected at the Environmental Change Network (ECN) site in Alice Holt Forest, Hampshire (0°50'W, 51°10'N). The site occupies a gently sloping plateau at an altitude of 110–125 m O.D., comprising the buildings of the Forest Research Station and coniferous and deciduous woodland covering an area of approximately 850 ha. Much of the forest consists of Corsican pine (*Pinus nigra* var. *maritima* (Ait.) Melville) plantation, but there are also 260 ha of oak (*Quercus petraea* L. and *Q. robur* L.). No major land-use changes have occurred at the site during the monitoring period, although in 1987 night-time security lighting was introduced to the area where the insect trap is located.

Macrolepidoptera were sampled using a standard Rothamsted insect light-trap. Samples were sent to Rothamsted Experimental Station, Hertfordshire, where the species caught each night were identified and collated. The Macrolepidoptera database for Alice Holt currently contains 93,215 records of individual specimens collected over 36 years. All records of the larger moth species were used to examine changes in abundance and species composition between 1966 and 2001. A sub-sample of 40 key species (Table 1) was selected from the database on the basis that they were resident species, occurred at least 200 times during the study period and whose diet was known to be biased toward broadleaved trees (Porter, 1997; Skinner, 1998). A further 34 non-key species (Table 2) whose diet was broad and not focused upon broadleaved trees (Porter, 1997; Skinner, 1998), and which occurred at a frequency of 200 specimens or more during the study period, were also selected. This sample was used to examine whether trends in abundance were restricted to the key species or were occurring more generally.

Rainfall (mm) and average daily dry air temperature (°C) recorded from 1964–2001 at the Forest Research meteorological station in Alice Holt forest were used in the analysis. The station is less than 40 m from the light-trap used to obtain Lepidoptera specimens.

Table 1. Macrolepidoptera defined as 'Key species' and known to favour broadleaved trees.

Scientific name and authority	Vernacular name
Conistra vaccinii (Linnaeus)	The Chestnut
Epirrita dilutata ([Denis & Schiffermüller])	November Moth
Orthosia cruda ([Denis & Schiffermüller])	Small Quaker
Chloroclysta truncata (Hufnagel)	Common Marbled Carpet
Cosmia trapezina (Linnaeus)	The Dun-bar
Erannis defoliaria (Clerck)	Mottled Umber
Agrochola lychnidis ([Denis & Schiffermüller])	Beaded Chestnut
Operophtera brumata (Linnaeus)	Winter Moth
Hydriomena furcata (Thunberg)	July Highflyer
Cymatophorima diluta hartwiegi (Reisser)	Oak Lutestring
Orthosia gothica (Linnaeus)	Hebrew Character
Colotois pennaria (Linnaeus)	Feathered Thorn
Xestia triangulum (Hufnagel)	Double Square-spot
Lomaspilis marginata (Linnaeus)	Clouded Border
Herminia tarsipennalis (Treitschke)	The Fan-foot
Ectropis bistortata (Goeze)	The Engrailed
Orthosia cerasi (Fabricius) (*stabilis* ([Denis & Schiffermüller]))	Common Quaker
Serraca punctinalis (Scopoli)	Pale Oak Beauty
Xanthia icteritia (Hufnagel) (*fulvago* (Linnaeus))	The Sallow
Opisthograptis luteolata (Linnaeus)	Brimstone Moth
Selenia dentaria (Fabricius) (*bilunaria* (Esper))	Early Thorn
Hemithea aestivaria (Hübner)	Common Emerald
Campaea margaritata (Linnaeus)	Light Emerald
Herminia nemoralis (Fabricius) (*grisealis* ([Denis & Schiffermüller]))	Small fan-foot
Falcaria lacertinaria (Linnaeus)	Scalloped Hook-tip
Cabera exanthemata (Scopoli)	Common Wave
Diarsia brunnea ([Denis & Schiffermüller])	Purple Clay
Odontopera bidentata (Clerck)	Scalloped Hazel
Poecilocampa populi (Linnaeus)	December Moth
Alsophila aescularia ([Denis & Schiffermüller])	March Moth
Agriopis aurantiaria (Hübner)	Scarce Umber
Eupsila transversa (Hufnagel) (*sateitia* (Linnaeus))	The Satellite
Eupithecia abbreviata (Stephens)	Brindled Pug
Alcis repandata repandata (Linnaeus)	Mottled Beauty
Euproctis similis (Fuessly)	Yellow-tail
Agrochola macilenta (Hübner)	Yellow-line Quaker
Cabera pusaria (Linnaeus)	Common White Wave
Dryobotodes eremita (Fabricius) (*protea* ([Denis & Schiffermüller]))	Brindled Green
Eupthecia vulgata vulgata (Haworth)	Common Pug
Peribatodes rhomboidaria ([Denis & Schiffermüller])	Willow Beauty

Data analysis

The records for each species across all years were collated and simple linear regression was used to identify trends in total moth numbers (all species combined) and total species, and the abundance of key species (N = 40) and non-key species (N = 34). Changes in species composition were quantified by comparing the number of species lost and gained from the data set during different time periods.

Trends in the number of species and climate data were analysed using linear regression, while trends in the abundance of moths and their relationship to the climate data were examined using a Poisson regression model (Crawley, 1993). To examine the relationship to the temperature and precipitation variables, the counts were regressed on year and on total precipitation and mean temperature occurring in the winter (December, January, February), spring (March, April, May), summer (June, July, August) and autumn (September, October, November) of the current year (t) and previous year (t-1). Data were analysed using GenStat release 6.1 (NAG, 2003).

Table 2. Macrolepidoptera defined as 'Non-key species, with broad diet requirements.

Scientific name and authority	Vernacular name
Spilosoma lubricipeda (Linnaeus)	White Ermine
Ochropleura plectra (Linnaeus)	Flame Shoulder
Idaea aversata (Linnaeus)	Riband Wave
Hoplodrina blanda ([Denis & Schiffermüller])	The Rustic
Agrotis exclamationis (Linnaeus)	Heart and Dart
Eupithecia pusillata pusillata [Denis & Schiffermüller]) (*sobrinata* (Hübner))	Juniper Pug
Diarsia mendica mendica (Fabricius) (*festiva* ([Denis & Schiffermüller]))	Ingrailed Clay
Xanthorhoe montanata montanata ([Denis & Schiffermüller])	Silver-ground Carpet
Rusina ferruginea (Esper) (*umbratica* (Goeze), *tenebrosa* (Hübner))	Brown Rustic
Xanthorhoe fluctuata (Linnaeus)	Garden Carpet
Ecliptopera silaceata ([Denis & Schiffermüller])	Small Phoenix
Photedes minima (Haworth) (*arcuosa* Haworth)	Small Dotted Buff
Hoplodrina alsines (Brahm)	The Uncertain
Hydraecia micacea (Esper)	Rosy Rustic
Diarsia rubi (Vieweg)	Small Square-spot
Idaea subsericeata (Haworth)	Satin Wave
Cybosia mesomella (Linnaeus)	Four-dotted Footman
Caradrina morpheus (Hufnagel)	Mottled Rustic
Cidaria fulvata (Forster)	Barred Yellow
Eupithecia pulchellata pulchellata (Stephens)	Foxglove Pug
Agrotis puta puta (Hübner)	Shuttle-shaped Dart
Cosmorhoe oscillata (Linnaeus)	Purple Bar
Idaea dimidiata (Hufnagel)	Single-dotted Wave
Idaea emarginata (Linnaeus)	Small Scallop
Thera obeliscata ((Hübner))	Grey Pine Carpet
Noctua pronuba (Linnaeus)	Large Yellow Underwing
Hypena proboscidalis (Linnaeus)	The Snout
Thera britannica (Turner)	Spruce Carpet
Euphyia unangulata (Haworth)	Sharp-angled Carpet
Semiothisa liturata (Clerck)	Tawny-barred Angle
Colostygia pectinataria (Knoch)	Green Carpet
Gymnoscelis rufifasciata (Haworth)	Double-striped Pug
Idaea trigeminata (Haworth)	Treble Brown Spot
Eilema lurideola (Zincken)	Common Footman

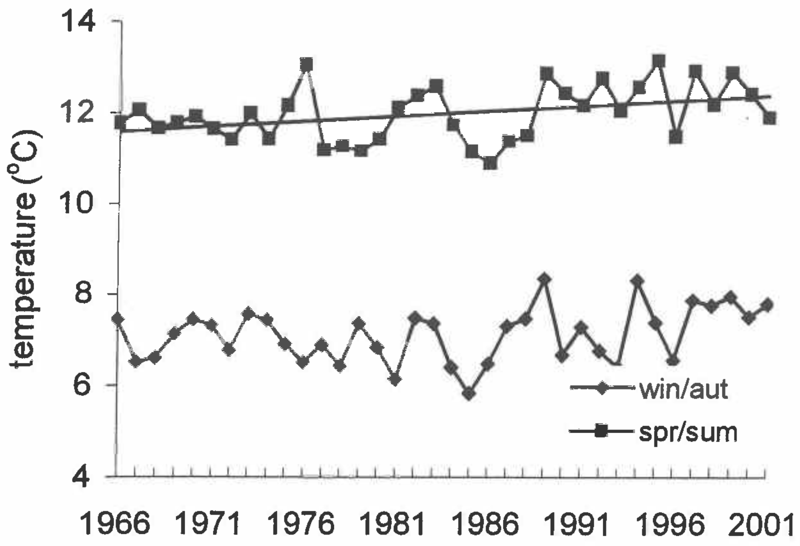

Fig. 1. Seasonal variations for average daily air temperature (°C). Fitted linear regressions for temperature: spring-summer: $R^2 = 0.13, p = 0.02$.

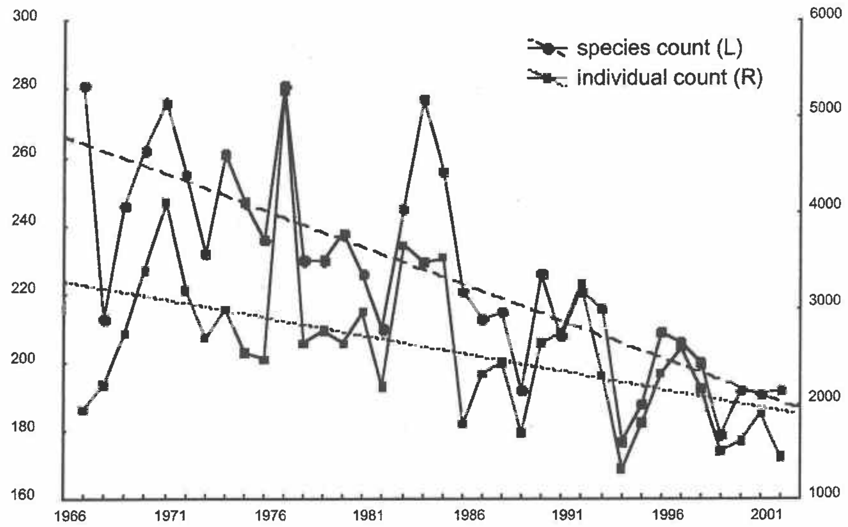

Fig. 2. Variation in the total numbers of individuals and species of Macrolepidoptera collected at Alice Holt, 1966–2001 (total numbers: $R^2 = 0.22, p = 0.003$; species numbers: $R^2 = 0.58, p < 0.0001$).

Results

Owing to a large variation in total precipitation between years, analysis of rainfall records between 1966 and 2001 yielded no statistically significant trends, though they broadly support the general picture of increasingly drier summers and wetter winters (Hulme *et al.*, 2002). In addition, trends toward warmer spring-summer and autumn–winter seasons are suggested by the average temperature data, though only those for spring-summer were significant (p = 0.02) with a slope of 0.023 (+/–0.009) (Fig. 1). These results are also consistent with general information about the changing climate in the region (Hulme *et al.*, 2002).

The total number of species declined significantly during the 1966–2001 period (p = 0.003 with slope –2.15 (+/–0.30), i.e., an average loss of about two species per year (Fig. 2).

The trend in total numbers of moths for key species showed an initial increase followed by a decline. For the non-key moths the initial increase was not significant (Fig. 3). However, restricting the data to after 1976, both groups showed similar declines with no significant difference between the two groups.

Examining the trend for the individual key species showed that only *Peribatodes rhomboidaria* ([Denis & Schiffermüller]) showed a significant increase while in general there was a tendency to show a decrease. Figure 4 shows a

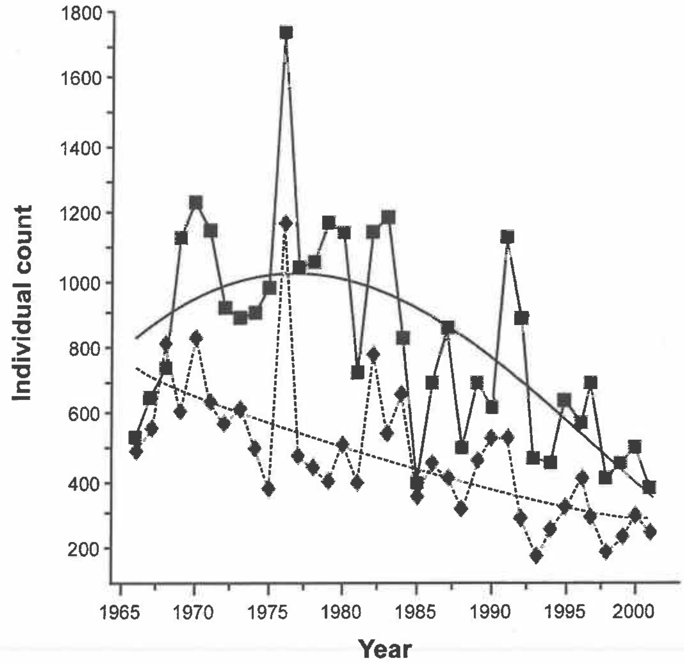

Fig. 3. Individual counts and fitted curves for key (■) and non-key (♦) species.

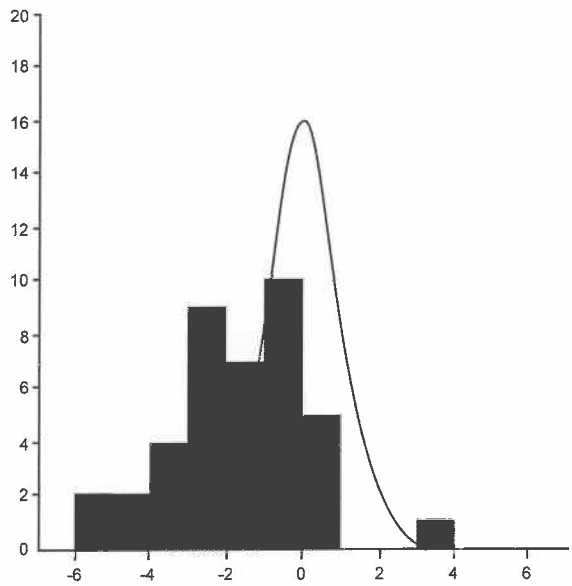

Fig. 4. Histogram of standardised regression trend coefficients for key species, and distribution curve under the null hypothesis.

histogram of the standardised coefficient (i.e. coefficient divided by its standard error) and the expected distribution if there were no trend.

Examining the relationship between climate and moth abundance, given the above trend, showed that both summer temperature with a positive slope and winter precipitation with a negative slope were significant (though the latter was not significant if data prior to 1976 were excluded). This can also be seen by looking at the slopes for individual species. Figure 5 shows the standardised coefficients for the eight climatic variables. For summer temperature there was a clear shift to the right (positive slope) while for winter precipitation there was a shift to the left (negative slope).

Based on information on those species whose numbers are supplemented by continental migrants (Table 3), Table 4 gives information on the proportion of semi-migratory species in the Lepidoptera samples. The results show no trend in the percentage of moth species made up by this group, thus declines in species with a migratory component appear to have been similar to purely residential ones.

Discussion

The results demonstrate that the number of species and the abundance of Macrolepidoptera at Alice Holt have decreased over the monitoring period. Given the trend toward warmer temperatures in the area, the results are contrary

Table 3. Largely resident species, but with their populations supplemented by migrants each year (from Skinner, 1998).

Scientific name and authority	Vernacular name
Tethea ocularis octogesimea (Hübner)	Figure of Eighty
Agrotis ipsilon (Hufnagel)	Dark Sword-grass
Peridroma saucia (Hübner)	Pearly Underwing
Noctua pronuba (Linnaeus)	Large Yellow Underwing
Polia hepatica (Clerck)	Silvery Arches
Discestra trifolii (Hufnagel)	The Nutmeg
Mythimna albipuncta ([Denis & Schiffermüller])	White-point
Hoplodrina ambigua ([Denis & Schiffermüller])	Vine's Rustic
Phlogophora meticulosa (Linnaeus)	Angle Shades
Dichonia aprilina (Linnaeus)	Merveille de Jour
Rivula sericealis (Scopoli)	Straw Dot
Parascotia fuliginaria (Linnaeus)	Waved Black
Rhodometra sacraria (Linnaeus)	The Vestal
Hylaea fasciaria (Linnaeus)	Barred Red
Plutella xylostella (Linnaeus)	Diamond-backed Moth
Lithophane leautieri hesperica (Boursin)	Blair's Shoulder Knot

Table 4. The proportion of total Macrolepidoptera individuals made up by species with a significant migratory component in each five-year interval from 1966 to 2000.

	Period						
	1966–70	1971–75	1976–80	1981–85	1986–90	1991–95	1996–00
Suspected migrants (% of total individuals)	3.6	2.8	3.5	4.4	4.8	3.5	4.0
Total no. of moth species (N)	358	354	347	344	328	314	299

to expectations that such changes should generally favour an increase in the number of Lepidoptera species and an increase in population numbers of many species. The results substantiate those of other studies that reveal a general 60% decline in Macrolepidoptera numbers since 1930 (Woiwod, 2003). Moth-trap data collected across various forests in Hungary between 1962 and 2000 also showed a 'definitive significant decreasing trend' in both numbers and species (Szentkirályi, Kazinczy & Leskó, 2001).

Among the sample of key-species showing a negative trend were *Operophtera brumata* and *Erannis defoliaria*, both known to be responsible for past episodes of broadleaved tree defoliation in the U.K. (Harding, 2002). The decline in abundance of these species suggests that currently and in the future there is a lower risk of defoliation. Other observations suggest that oak (*Q. robur*) and other broadleaved trees in woodlands have suffered less defoliation in recent years (Harding, 2002). Only *Peribatodes rhomboidaria* (Esper) showed a positive trend. There is no evidence that this species has been associated with serious defoliation in the U.K.

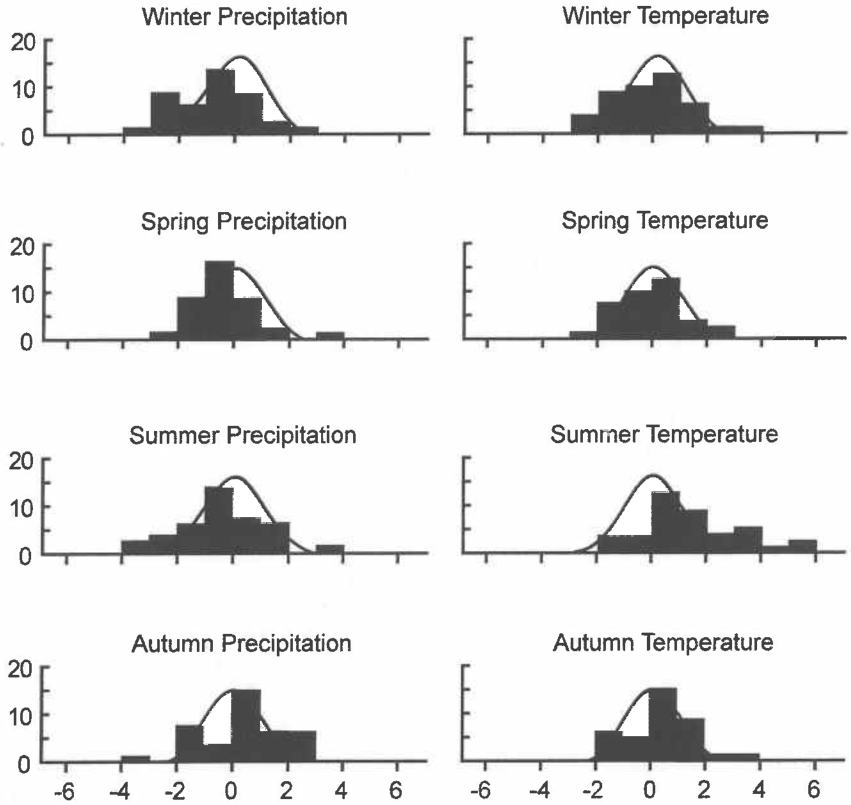

Fig. 5. Histograms of standardised regression coefficients on climatic variables for key species, and distribution curves under the null hypothesis.

Analyses of the relationship of the climate data with the yearly abundance data for the key species confirmed the well-documented positive relationship between abundance and temperature, particularly with summer temperature in the current year (Pollard & Yates, 1983; Pollard, 1988).

The overall decline in Macrolepidoptera numbers and diversity revealed by our study suggests that other factors are overriding the positive effects of higher temperatures for species. Several other studies have suggested that changes in rainfall may be affecting Lepidoptera survival (Warren, Pollard & Bibby, 1986; Pollard, 1988), but little evidence of this was found in our analysis. Shifts in tree phenology, as a response to changes in the seasonal pattern of temperatures (Murray, Cannell & Smith, 1989; Sparks & Yates, 1997), might also affect the survival of Lepidoptera larvae by advancing or delaying budburst (Dewar & Watt, 1992; Visser & Holleman, 2001). However, the decline in moth numbers at Alice Holt, and the reasons for extinctions of resident species, remain largely unknown. Even though habitats within Alice Holt forest appear to have changed little over the last 40 years, wider changes in land-use in the area surrounding the forest may have affected moth populations at the landscape scale. Only analysis of data on Macrolepidoptera abundance from a range of sites will indicate whether the declines observed at Alice Holt are a local phenomenon, or are part of a general trend.

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